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Variability in the production of wound ethylene in bananas from the French West Indies

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Abstract

The main banana quality problems in the French West Indies are early ripening of fruit during storage and wound anthracnose. The extent of these post-harvest problems varies markedly for bananas grown in lowland areas, in contrast with those grown in the highlands. These quality problems are common during the second half of the year, when the fruit develops during the hot wet season. An experiment was carried out in areas with differing soils and climate, through two seasons with different rainfall patterns. The results showed that in the wet season, lowland fruit was mechanically more fragile and produced more wound ethylene than highland fruit (about 1850 nl/kg for lowland bananas, and 1000 nl/kg for highland bananas). The malic acid concentration of the fruit was quite closely correlated with this wound ethylene production, especially in fruit grown at low elevation ($r = 0.80$). However, there was no correlation between the ACC concentration of the fruit and wound ethylene production. On the other hand, there was a weak correlation between the Mn concentration and wound ethylene production in lowland bananas. These results indicate that climatic conditions during fruit growth has an important influence on fruit quality and post-harvest physiology.

Keywords: Banana; *Musa*; Ethylene; Malic acid; 1-Aminocyclopropane-1-carboxylic acid (ACC)

1. Introduction

Export banana production in the Caribbean region is affected by high variability in the fruit quality (Marriott, 1980). The presence of bananas that are already ripe before being placed in ripening rooms and the development of large wound anthracnose lesions on the peel are factors that are particularly detrimental to fruit quality (de Lapeyre de Bellaire,

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1999). These quality problems chiefly arise during the rainy season, notably in lowland production areas. Although fruit handling during harvest and packing, and refrigeration conditions during transport may exacerbate these disorders, the seasonal and geographical variability is linked with the development of the fruit quality potential in the field (Chillet and de Lapeyre de Bellaire, 1996). The fruit quality potential can thus vary substantially, depending on the production area and the cultural techniques used by the growers. This variability in the banana quality potential at the harvest stage is expressed by variability in certain physiological characteristics of the fruit, e.g. the duration of the green-life (Marriott et al., 1979) and shelf-life (Seberry and Harris, 1994), the hardness of the peel (Chillet and de Lapeyre de Bellaire, 1996) and pulp (Deullin, 1966; Chillet et al., 1998) and the susceptibility to wound anthracnose (Chillet et al., 2000).

Fruit handling during packing operations can cause peel bruising, leading to the problems listed above. Indeed, wounds induced by shocks or crushing foreshortens the green-life and shelf-life of many fruits and vegetables (Poenicke et al., 1977; Harvey, 1978; Ferris et al., 1994). This shortening of fruit-life is the result of the release of ethylene produced by the fruit in response to wounding (Abeles et al., 1992).

Ethylene is a plant hormone that is involved in the ripening of climacteric fruits such as bananas (Burg and Burg, 1965). Furthermore, ethylene may stimulate the development of various post-harvest diseases in certain fruit species such as bananas (de Lapeyre de Bellaire et al., 2000).

The main hypothesis put forward to explain the observed fruit quality variations is that they may depend on variations in fruit fragility and on wound ethylene synthesis. These patterns would thus depend on the fruit growth and development conditions, and on the fruit age at harvest.

The mineral composition of fruits could influence their mechanical characteristics, for instance in apples calcium deficiency leads to weakening of the fruit (Conway, 1989).

The biochemical composition of the fruit could influence ethylene production after wounding. If the fruits are not the same physiological age at harvest time, the oldest and thus ripest ones will likely be the most fragile. Certain biochemical indicators, such as 1-aminocyclopropane-1-carboxylic acid (ACC), an ethylene precursor, and malic and citric acids, could help to determine the extent of fruit ripeness (Inaba and Nakamura, 1988; Selli and Sansavini, 1995).

The aim of this study was to explore this possible variability in wound ethylene production in bananas grown under different soil and climatic conditions, and to investigate relationships between environmental conditions, mechanical and biochemical characteristics of the fruit and the wounding response.

2. Materials and methods

2.1. Experimental plots

Three experimental plots planted with banana (*Musa acuminata*, triploid, subgroup Cavendish, cv Grande Naine) were set up in the Guadeloupian banana cropping area (French West Indies) under contrasting soil and climatic conditions.

Two plots were located in a lowland zone on halloysitic soil (Changy [CHA] and Mineurs [MIN] at 30 m elevation). This soil type was chosen because it is representative of that found in lowland banana growing areas in Guadeloupe, where marked seasonal variations in fruit quality are common. The climate of this zone is characterised by a very wet season and a so-called dry season, with an alternation of very wet and very dry periods.

One plot was located in the highland zone, on andosols of the leeward slope (Matouba [MAT] at 600 m elevation). This soil type was chosen because it is representative of that found in highland banana growing areas in Guadeloupe, where there is very little variation in fruit quality. The climate of this zone is characterised by the absence of a marked dry season.

2.2. Fruit harvest

Ten harvest dates were chosen, five during the rainy season (rainfall above 1000 mm over a 100 day period preceding harvest for the lowland CHA and MIN plots, and above 1800 mm for the highland MAT plot) and five during the dry season (rainfall below 600 mm over a 100 day period preceding harvest for the CHA and MIN plots, and below 900 mm for the MAT plot).

For each harvest date, 10 banana plants were selected for their uniformity with respect to developmental stage and bunch shape. The third hands from 10 bunches were sampled. Only the middle fingers were used for the laboratory analyses, since they are considered to be comparable (Liu, 1976). The harvest stage was defined by the diameter of the middle external fruit of the fourth hand, which should be 34 ± 1 mm (commercial grade).

Ten bananas per harvested hand (five internal and five external) were sampled. The peduncle wound was then healed using wax. The fruits were then stored for 24 h after cutting in a ventilated chamber at 25 °C so as to eliminate ethylene produced around the cutting zone. Each hand represented one replication.

2.3. Analysis of wound ethylene production

Four bananas (two internal and two external) were wounded using a penetrometer. The wound was produced by compressing the peel of the fruit for 4 s. This was done with a bullet-shaped tip which compressed the peel in a standardised manner, and 18 wounds were made on each fruit (six on each of the three sides).

After this treatment, the bananas were weighed and placed in 3-l glass jars, which were then hermetically sealed and fitted with a sampling septum and an internal ventilation system using magnetic bars. Four bananas from the same hand were placed in each jar. The jars were stored in a controlled environment chamber at 25 °C.

Four unbruised bananas (two internal and two external) were weighed and placed in glass jars (as above) to serve as controls (for basal ethylene production). These fruits were also stored at 25 °C.

After 16 h of storage, duration of ethylene production by the fruit after wounding (Dominguez and Vendrell, 1993), 250 μl of gas was withdrawn and analysed by gas chromatography (HP 5890; column GS-Q, 30 m, from J&W; oven 50 °C, FID). Three measurements per jar were made for each replicate. Measurements of O_2 and CO_2 were

also made using a CARBOX Y analyser (Pekly-Hermann Morritz) in order to check that levels in the jars were similar by the end of the storage period.

2.4. Mechanical measurements

Two bananas (internal and external) were used for mechanical measurements to characterise fruit fragility. The parameters analysed were peel and pulp hardness (Chillet and de Lapeyre de Bellaire, 1996).

2.5. Mineral and biochemical analysis of fruits

A transverse section was sampled from each of the fruit used for the mechanical analysis, and frozen in liquid nitrogen prior to storage at $-20\,^{\circ}$C. The mineral concentration (N, P, K, Ca, Mg, Na, Cl, Mn, Fe) of the peel and pulp were analysed after lyophilisation.

ACC concentrations in the peel and pulp were measured after ACC extraction with ethanol from 3 g of the frozen samples (0.3 g/fruit $\times$ 10 fruits/plot). Measurements were carried out using the technique described by Lizada and Yang (1979). Malic and citric acid concentrations in the pulp were analysed using the technique described by Pintro et al. (1997).

2.6. Statistical analysis

For each harvest date, the mean of 10 replications was calculated for each of the parameters analysed. This mean value was then used for the replicate x (x ranged from 1 to 5 for each season studied). These calculated values were used for the analysis of variance (Newman–Keuls test at the 5% probability level) and for calculating correlation coefficients using the STAT-ITCF (1991) software package.

3. Results

3.1. Variations in wound ethylene production

Table 1 shows the means of five samplings per plot and per season. These data indicate that:

- there were marked geographical variations in wound ethylene synthesis in the rainy season; fruit from lowland areas, principally from CHA, produced significantly more ethylene for a given wound than fruit from the highland plot;
- seasonal variations were significant for the lowland plots, CHA (at 5%) and MIN (at 10%), and not significant for fruit grown on the highland plot that we studied.

Note that ethylene measured in glass jars only represented wound ethylene production. Indeed, control fruit without any bruising did not produce detectable amounts of ethylene during storage.

Table 1
Ethylene production (nl/kg_{FW}) per fruit from two soil/climate zones after wounding the peel with a penetrometer[a]

	Wound ethylene (nl/kg)		
	Rainy season	Dry season	Seasonal variation
Changy (CHA)	1850 ± 430 (a)	1290 ± 190 (a)	S ($P = 0.041$)
Mineurs (MIN)	1460 ± 350 (ab)	1100 ± 80 (ab)	NS ($P = 0.072$)
Matouba (MAT)	1010 ± 180 (b)	990 ± 70 (b)	NS ($P = 0.817$)
F	6.30	5.81	
P	0.0134	0.0171	

[a] Each value is the mean calculated from values obtained from five harvests of 10 bunches made each season at each site. *F*, *P* and (*x*) are the values of the *F*-test, its probability, and the uniform groups defined in the analysis of variance (at 5%) by the Newman–Keuls test, respectively. When the seasonal variations were significant ($P < 0.05$), they are denoted S, and otherwise NS.

3.2. Variation in the mechanical measurements

Table 2 shows the means obtained for peel and pulp hardness for the three plots studied. These results indicate that:

- there was high geographical variation in the wet season for peel and pulp hardness, with fruit from the highland plot being significantly harder;
- these differences were reduced in the dry season; there was no significant difference in fruit peel hardness; there was still a difference in pulp hardness, but less than in the wet season;
- there were seasonal variations in peel hardness for fruit from the lowland plots: peel of these fruits was significantly harder in the dry season. On the other hand, there was no significant seasonal variation in pulp hardness, except for the MIN plot.

3.3. Relationships between mineral elements and wound ethylene production

There was no clear correlation between wound ethylene production and the mineral element concentration in fruit peel. However, there was a slight correlation between the Mn

Table 2
Peel and pulp hardness (N) of fruits from two soil/climate sites measured with a TA-XT2 penetrometer[a]

	Hardness of the pulp (N)			Hardness of the peel (N)		
	Rainy season	Dry season	Seasonal variation	Rainy season	Dry season	Seasonal variation
Changy (CHA)	19.24 ± 0.83 (b)	20.77 ± 0.53 (b)	S ($P = 0.014$)	46.45 ± 1.56 (b)	54.26 ± 1.75	S ($P = 0.000$)
Mineurs (MIN)	19.84 ± 0.75 (b)	20.55 ± 0.79 (b)	NS ($P = 0.261$)	46.46 ± 4.45 (b)	54.02 ± 1.53	S ($P = 0.012$)
Matouba (MAT)	22.17 ± 0.60 (a)	22.25 ± 0.40 (a)	NS ($P = 0.816$)	54.25 ± 2.68 (a)	55.80 ± 1.35	NS ($P = 0.335$)
F	17.66	9.73		8.26	1.54	
P	0.0003	0.0032		0.0056	0.2528	

[a] Each value represents a mean calculated from values obtained from five harvests of 10 bunches at each site. *F*, *P* and (*x*) are the values of the *F*-test, its probability, and the uniform groups defined in the analysis of variance (at 5%) by the Newman–Keuls test, respectively. When the seasonal variations were significant ($P < 0.05$), they are denoted S, and otherwise NS.

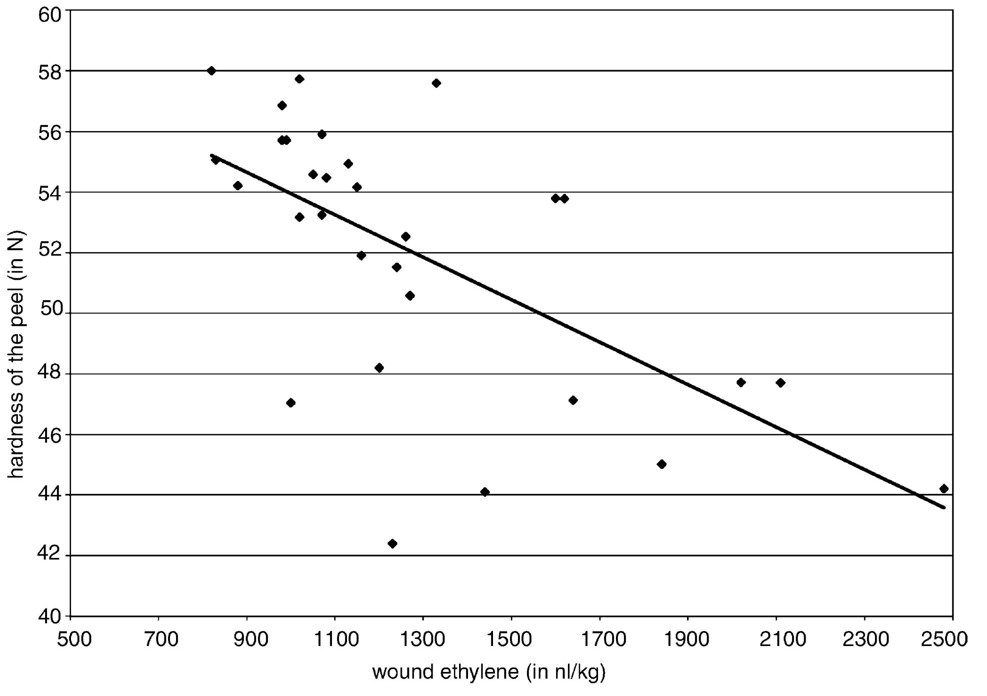

Fig. 1. Wound ethylene production (nl/kg$_{FW}$) by fruits from the three sites related to their peel hardness (N) measured by a penetrometer. Each point is the mean of 10 replicates from each harvest.

concentration in fruit peel and the wound ethylene production ($r = 0.65$). This coefficient is low but suggests a possible relationship.

3.4. Relationship between fruit hardness and wound ethylene production

Fig. 1 highlights the relationships between the wound ethylene produced by fruit and the mechanical measurements of peel hardness. Although the correlation is poor ($r = -0.60$), these results indicate that wound ethylene production is lower in harder fruit.

3.5. Relationships between wound ethylene production and ACC concentration in fruit

No relationship was found in this experiment between wound ethylene production and the ACC concentration in the peel ($r = 0.10$) or pulp ($r = 0.45$).

Table 3 shows that there was no significant variation in the ACC concentration in fruit related to the geographical conditions, nor were there significant variations related to season ($P > 0.05$).

Table 3
ACC concentration (nmol/g_{FW}) of peel and pulp of fruit from the three soil/climate sites[a]

	ACC in the peel and in the pulp (nmol/g_{FW})			
	Rainy season		Dry season	
	Peel	Pulp	Peel	Pulp
Changy (CHA)	0.01 ± 0.02	0.14 ± 0.11	0.13 ± 0.21	0.11 ± 0.09
Mineurs (MIN)	0.00 ± 0.00	0.13 ± 0.09	0.03 ± 0.06	0.12 ± 0.10
Matouba (MAT)	0.03 ± 0.06	0.10 ± 0.08	0.00 ± 0.00	0.04 ± 0.04
F	0.78	0.23	1.28	1.00
P	0.4842	0.802	0.3142	0.3998

[a] Each value represents a mean calculated from values obtained from five harvests of 10 bunches at each site. *F*, *P* and (*x*) are the values of the *F*-test, its probability, and the uniform groups defined in the analysis of variance (at 5%) by the Newman–Keuls test, respectively.

3.6. Relationships between wound ethylene production and malic acid concentration in fruit

Fig. 2 shows the relationships between the fruit pulp malic acid concentration and wound ethylene production for the two soil and climatic zones (a), and for the lowland zone (b). The correlations are not close ($r = 0.69$ in Fig. 2a, and $r = 0.80$ in Fig. 2b), but nevertheless show a trend, particularly for the lowland zone.

Concerning the citric acid concentration, correlation coefficients (between citric acid concentration and wound ethylene production) were lower but show the same trend ($r = 0.43$ for the three plots, and $r = 0.67$ for the lowland plots).

4. Discussion

This experiment demonstrated variations in the production of wound ethylene that were dependent on the harvesting season and the production zone. These results clearly show that fruits of the same commercial grade can produce, for a standardised wound, quite different amounts of wound ethylene. In the rainy season, fruits from lowland areas generally produce much more ethylene than those from the highlands. Nevertheless, variability in wound ethylene biosynthesis was noted for fruits from the lowlands during this season. Fruits from CHA produced more ethylene after wounding than fruits from MIN. Earlier experiments on other aspects of fruit quality, such as green-life and sensitivity to anthracnose disease, also showed that there is always variability during this season and that it depends on cultural practices (Chillet et al., 2000). There were fewer differences between zones in the dry season due to a drop in wound ethylene production by lowland fruit. In lowland banana plantations, there can be considerable seasonal variations in wound ethylene production.

The second finding of this experiment is the relationship between wound ethylene production and peel hardness. Ethylene production was lower in fruit with harder peel. This suggests that fruit with the lowest hardness values will suffer the greatest peel damage

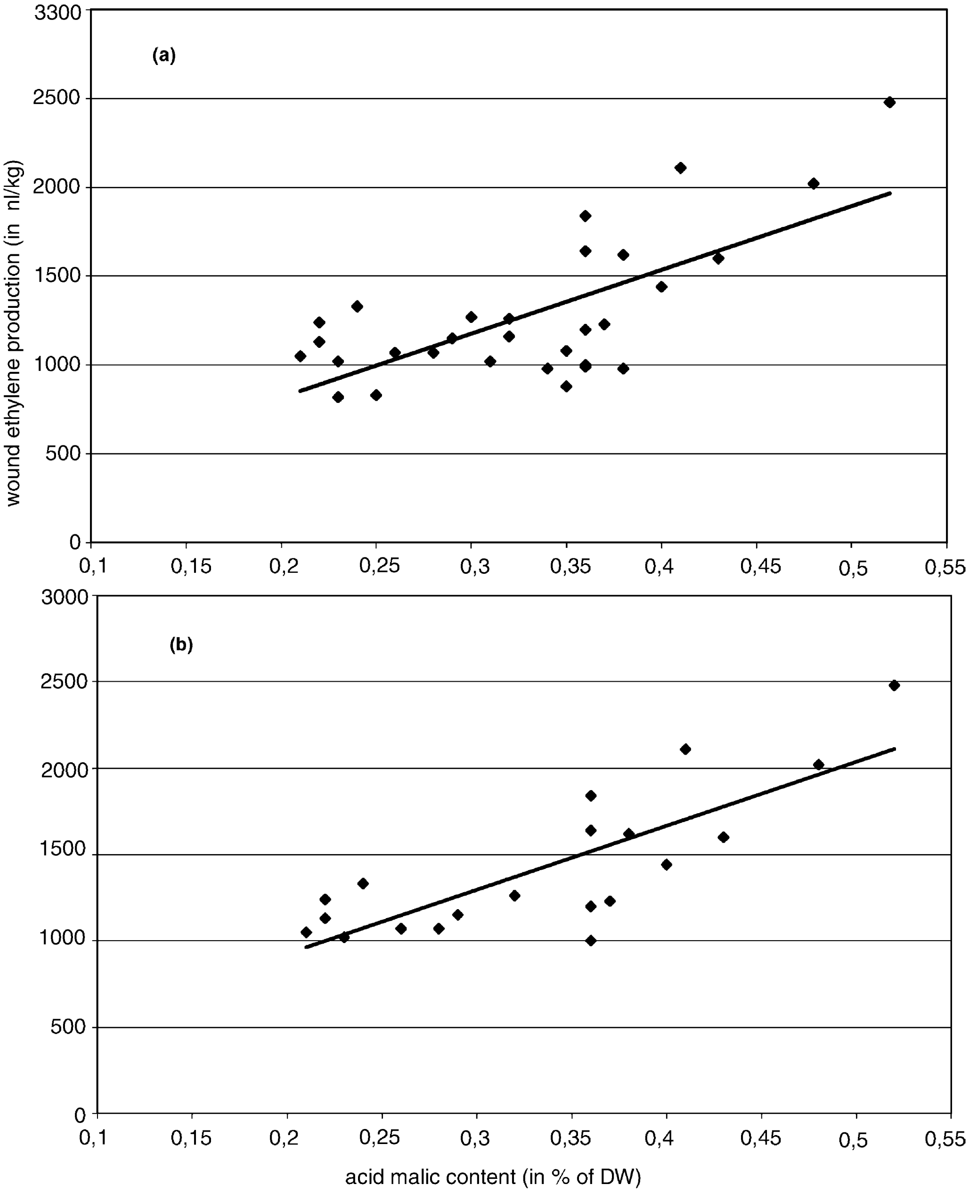

Fig. 2. Wound ethylene production (nl/kg_{FW}) by fruits from the three sites (a) and by fruits from the lowland zone (b) related to their pulp malic acid concentration (% DW). Each point is the mean of 10 replicates from each harvest.

following bruising by compression. The high ethylene production of these fragile fruits could thus reflect the extent the damage caused by fruit peel compression.

In this experiment, we analysed fruit from another Cavendish banana variety (Poyo), which is commonly produced in highland parts of the French West Indies. This variety

showed low wound ethylene production (about 800 nl/kg in both seasons) and very high peel hardness (about 56 N in both seasons). Nevertheless, our results did not allow us to distinguish between the varietal effects and those related to the environmental conditions.

A relationship was also noted between the malic acid concentration in the fruit and the production of wound ethylene. Fruits which produced high quantities of wound ethylene had the highest malic acid concentrations. This could be explained by the fact that the malic acid concentration could be an indicator of the physiological age of the fruit. In fact, for a climacteric fruit like peach, it has been shown that there is an accumulation of malic acid in the fruit during growth and ripening (Souty et al., 1999), and that fruit maturity is more advanced when the malic acid concentration is higher (Liverani and Cangini, 1991). If the malic acid concentration is also an indicator of fruit maturity in bananas, fruits with a high concentration should therefore be physiologically older than those with a lower concentration, although of the same grade. These would be fruits that have undergone severe stress during their growth.

No relationship was found between wound ethylene production and ACC concentrations in peel and pulp. The amount of ethylene produced following bruising by compression therefore does not depend on the amount of ACC present before the bruising occurs.

The mechanical fragility of lowland fruit in the rainy season, correlated with wound ethylene production, could account for the quality problems which appear seasonally in these growing regions. The problems of consignments arriving ripe, usually linked to early ripening of fruit due to late harvesting, might be accentuated by rapid wound ethylene production of fruit bruised during harvesting and packing. Ethylene released by these fragile and bruised fruits could actually result in the ripening of all bananas in a particular box, or even in a whole container. Wound anthracnose caused by *Colletotrichum musae* also appears during the rainy period. Fruit from these lowland zones are the most susceptible to this disease (Chillet et al., 2000). The vulnerability of these fruits to mechanical handling, and the high wound ethylene production linked to it, could enhance fruit susceptibility to *C. musae*.

Variations observed in the synthesis of wound ethylene of some bananas from lowland areas underlines the importance of the growing conditions on the post-harvest quality of the fruit. The fragility of this fruit in the rainy season could result from stressful growing conditions for banana plants. In fact, when rainfall is heavy in this growing region, hypoxic and anoxic conditions set in when the soil is compacted or drainage is inadequate. In these excess water conditions, oxidised forms of manganese present in these soils are reduced and rapidly absorbed by banana plants (Dorel, 1993). In our experiments, we demonstrated a weak relationship between the fruit Mn concentration and wound ethylene production. Two hypotheses could be put forward to explain this relationship. The first is that a high Mn concentration in fruit can influence fruit ripening. Turner and Barkus (1982) have showed that high Mn supply had no effect on the fruit growth rate, but decreased the green-life of the fruit. It has also been demonstrated that Mn activates the conversion of ACC into ethylene (Penel et al., 1990). Because of the high Mn level, this kind of fruit could be more mature and produce more ethylene after wounding. The second hypothesis is that these high Mn concentrations might be an indicator of anoxic environmental conditions. In many plants, these anoxic conditions lead to activation of the ethylene biosynthesis pathway in the whole plant (Jackson, 1985). This ethylene synthesis during growth stress could be

responsible for modifying the mechanical characteristics of the fruit, leading to peel softening. Moreover, these stress conditions might cause physiological changes leading to a slowing down of plant growth (in Nilsen and Orcutt, 1996). This slowing down of fruit growth could delay the harvest date, i.e. fruit harvest would then be at a more advanced stage of maturity. The correlation found in this experiment between malic acid and wound ethylene could be explained by the fact that the physiologically oldest fruits are the most fragile, i.e. those that have developed during stressful growing conditions.

In conclusion, it seems that some fruit produced at low elevations during the rainy season have soft peel with a high Mn and malic acid concentration, producing large amounts of wound ethylene. Such fruit might originate from plants that have undergone stressful growing conditions, particularly anoxic conditions. Controlled environment experiments should be carried out to test this hypothesis.

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